

PHYLOGENY AND RELATIONSHIPS OF THE *PAPILIO FUSCUS* GROUP OF SWALLOWTAILS (LEPIDOPTERA: PAPILIONIDAE)

By D. L. Hancock

National Museum, P.O. Box 240, Bulawayo, Zimbabwe

Abstract

The *Papilio fuscus* group of Indo-Australian butterflies is considered to comprise seven species, placed in two subgroups; viz: (1) *P. hipponous* C. & R. Felder; *P. pitmani* Elwes & de Nicéville; *P. fuscus* Goeze; *P. canopus* Westwood and (2) *P. albinus* Wallace; *P. hysicles* Hewitson, *stat. rev.*; *P. woodfordi* Godman & Salvin. Subgroup (1) is considered to be of Sundaland origin, whilst subgroup (2) is of Papuan origin. The *fuscus* group is closely related to the *aegeus* and *godeffroyi* groups.

Introduction

Munroe (1961) defined the *fuscus* group as having the 'adult tailed, black with more or less well-defined white postmedial band, somewhat expanded in costal half of hind wings' and 'larva smooth, green variegated with brown, without tubercles or eye-spots; hosts Rutaceae.' He placed *fuscus* Goeze and *canopus* Westwood in this group and tentatively included *diophantus* Grose-Smith, *antonio* Hewitson, *noblei* de Nicéville, *albinus* Wallace, *hipponous* Felder, *sakontala* Hewitson, *jordani* Fruhstorfer and *walkeri* Janson.

Of Munroe's tentatively included species, *albinus* and *hipponous* are confirmed as members of the group: the remainder are excluded pending further study, particularly of the male genitalia. Of these, *diophantus*, *antonio* and *noblei* are provisionally associated with the *helenus-nepheles* assemblage and *jordani* is provisionally included in the *polytes* group. The remaining species, *walkeri* and *sakontala*, appear to be of hybrid origin, suggested by their pattern, wing shape and abbreviated tails, plus their being known by only one and two males respectively. One of the parent species is likely to be *polytes* Linnaeus in both cases; the other parents cannot at present be ascertained, as *polytes* is able to hybridize with many species (Ae, 1979).

Munroe (1961) defined the *woodfordi* group, which is here considered to be an integral part of the *fuscus* group, as having 'adult tailless, black and white' with 'larva lacking saddle and metathoracic band, with band of first abdominal segment narrow, oblique and raised, and with a pair of dorsal tubercles on prothorax and another on 9th abdominal segment; hosts Rutaceae'. He placed *woodfordi* Godman & Salvin and 'probably' *ptolychus* Godman & Salvin and *erskinei* Mathew in this group.

Racheli (1980) placed *ptolychus* as a subspecies of *woodfordi* and showed *erskinei* to be a subspecies of *bridgei* Mathew, a member of the *aegeus* group.

Munroe's definition of the *fuscus* group is not quite accurate: the adult is sometimes tailless and larval tubercles, although small, do exist dorsally on the prothorax and 9th abdominal segment.

Although the pattern of *woodfordi* is distinctive, characters of the male genitalia and immature stages show its close affinity with the *fuscus* group.

The *fuscus* group

The *Papilio fuscus* group can be re-defined as follows:—

Sexes similar, non-mimetic; pattern black or brown with or without a cream or white band or subapical spots on fore wing, generally with well-developed, often complete, broad or narrow cream or white postdiscal band on hind wing; submarginal pale spots absent or secondarily derived from red spots; hind wing with red and blue spots generally present; spatulate tail present or absent; male fore wing without androconia; thorax and abdomen generally with yellow lines, two lateral and one ventral lines on abdomen. Male genitalia with clasper (= harpe) apically produced into a narrow or broad, usually serrate, dorsal lobe. Mature larva solitary, variable in colour, green or orange-brown; metathoracic band and eye-spots lacking; brown band on 1st abdominal segment often present; pale patches often present on abdominal segments 2-4 and 7-8; white or blue abdominal segmental spots often present; tubercles present on prothorax and abdominal segment 9, sometimes also on segment 8. Pupa smooth; usually green; curved; thoracic protuberance a low hump. Larval food plants Rutaceae.

The seven species can be divided into two subgroups, based on the shape of the apical dilation to the male clasper. In the *fuscus* subgroup this dilation is a long, slender, serrate plate; in the *albinus* subgroup it is broad and knob-like. So far as is known, the brown form of the larva occurs only in species of the *fuscus* subgroup.

FUSCUS SUBGROUP

Papilio hipponous C. & R. Felder

Papilio hipponous C. & R. Felder, 1862, *Wien. ent. Mon.* 6: 283.

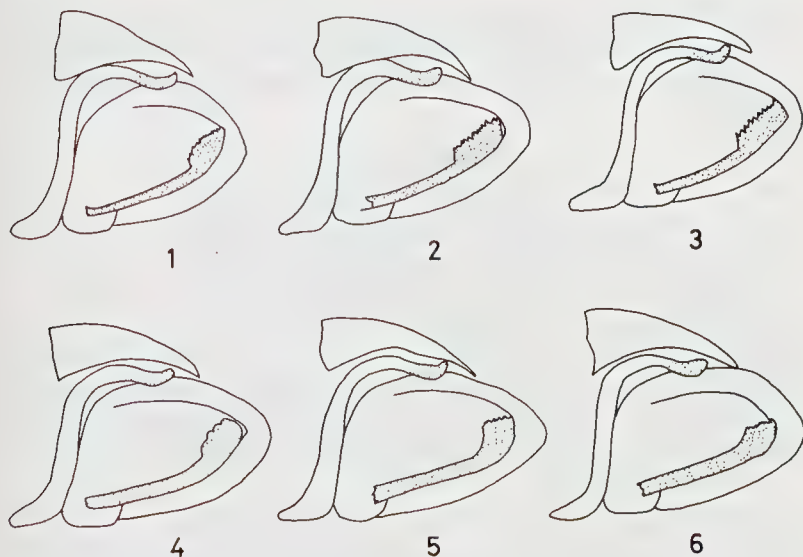
Type localities: Luzon; Mindanao (Philippines).

Fore wing generally with pale postdiscal band present above but often faint, represented below by a pair of pale spots in spaces 1b and 2; hind wing pale band relatively narrow, entire, usually slightly broader in spaces 4, 5 and 6; tail present; hind wing underside with a complete series of red submarginal spots and with blue spots in a complete series, reduced or absent.

Male genitalia (Fig. 1) typical of the subgroup.

Distribution: Two subspecies are currently recognised:— *P. h. hipponous* throughout the Philippines and Palawan; *P. h. lunifer* Rothschild on Sangir Island.

Immature stages: Described by Ae (1977). Mature larva very similar to that of *fuscus* and *canopus*, being either green or orange-brown with paler patches and abdominal blue or white spots, but has tubercles only on prothorax and ninth abdominal segment. Pupa green and smooth. Larval food plants Rutaceae.



Figs 1-6. Male genitalia (with left valve removed) of: (1) *Papilio hipponous*; (2) *P. fuscus*; (3) *P. canopus*; (4) *P. albinus*; (5) *P. hypsicles*; (6) *P. woodfordi*.

Papilio pitmani Elwes & de Nicéville

Papilio (*Laertias*) *pitmani* Elwes & de Nicéville, 1886, *J. Asiat. Soc. Bengal* 54: 434.

Papilio pitmanni Rothschild, 1894, *Novit. Zool.* 1: 685.

Type locality: Tavoy (Tenasserim, S. Burma).

Fore wing without pale postdiscal band above, present below as a pair of pale spots in spaces 1b and 2, as in *hipponous*; hind wing pale band broad to very broad in spaces 4, 5 and 6, narrow or reduced in spaces 1b, 2 and 3, better developed below; tail present; hind wing underside with a complete series of red submarginal spots but blue spots absent.

Male genitalia not studied.

Distribution: Two subspecies are recognizable:—*P. p. pitmani* has a relatively narrow hind wing pale band and is known from S. Burma and Thailand; *P. p. duboisi* Salvaza, comb. n. has the hind wing pale band broadened anteriorly and reduced posteriorly and is known only from Vietnam [Tao, Vinh province, N. Vietnam (type locality *vide* Dubois & Salvaza, 1921); Trang Bom Forest, NE of Saigon, S. Vietnam (A. Bedford Russell, pers. comm.)]. This subspecies probably also occurs in adjacent areas of Laos.

Immature stages: Unrecorded.

Comments: This species is sometimes regarded as a subspecies of *P. hipponous* and the two are certainly closely related. In view of the morphological

differences between *pitmani* and *hipponous*, and their distribution patterns (c.f. *antonio* and *noblei*), they are here maintained as separate species.

Identity of the Trang Bom Forest specimen has been confirmed by examination of photographs.

Papilio fuscus Goeze

Papilio Eques Achivus fuscus Goeze, 1779, *Ent. Beytr.* 3(1): 87.

Papilio Eques Achivus cinereomaculatus Goeze, 1779, *l.c.*: 88.

Papilio Eques Trojanus severus Cramer, 1782, *Pap. Exot.* 3: 153.

Achillades severus (Cramer); Hübner, 1816, *Verz. bek. Schm.*: 85.

Papilio severus Cramer. Godart, 1819, *Enc. Meth.* 9: 68.

Papilio castaneus var. *cinereomaculatus* Goeze; Kirby, 1877, *Cat. Diurn. Lep.*: 810.

Papilio cinereomaculatus Goeze; Ribbe, 1890, *Iris* 2: 208.

Type locality: S. Moluccas (? Amboina).

Fore wing with or without pale postdiscal band, when present generally reduced; hind wing pale band broad in spaces 4, 5 and 6, often reduced or absent in spaces 1b, 2 and 3; tail present; hind wing underside with red and blue spots generally present, often reduced.

Male genitalia (Fig. 2) typical of subgroup.

Distribution: This species has the widest distribution of the group, occurring from the Andaman Islands and Malaya to the Solomons and north-eastern Australia. Numerous subspecies have been described; their precise limits are currently under investigation by others (J. Haugum, pers. comm.).

Immature stages: Described by Straatman (1963) and Common and Waterhouse (1981). Mature larva green or orange-brown with paler patches and abdominal blue or white spots often present; tubercles present on prothorax and abdominal segments 8 and 9. Pupa green and smooth, with prominent anterior processes. Larval food plants Rutaceae.

Papilio canopus Westwood

Papilio canopus Westwood, 1842, *Ann. Mag. nat. Hist.* 9: 38.

Type locality: Melville Island (N. Australia).

Fore wing with pale postdiscal band well-marked or reduced; hind wing pale band relatively narrow becoming broader in *c. tenimberensis* Rothschild, generally entire; tail present or absent; hind wing underside with red and blue spots generally present, often reduced.

Male genitalia (Fig. 3) typical of the subgroup.

Distribution: This species occurs in the Lesser Sunda Islands and north-western Australia. Eight subspecies are currently recognised:—*canopus* (north-western Australia and Northern Territory); *tenimberensis* Rothschild (Tenimber & Baber); *vollenhovii* Felder (Timor); *croton* Fruhstorfer (Damar); *canopinus* Rothschild (Romang and Leti Is.); *hypsiclides* Rothschild (Wetar); *alorensis* Rothschild (Alor) and *umbrosus* Rothschild (Sumbawa).

Immature stages: Described by Common and Waterhouse (1981); mature larva and pupa as for *fuscus*. Larval food plants Rutaceae.

Comments: This species is very closely related to the allopatric *fuscus* and the two may be conspecific.

ALBINUS SUBGROUP

Papilio albinus Wallace

Papilio albinus Wallace, 1865, *Trans. Linn. Soc. Lond.* 25: 49.

Papilio severus var. *albinus* Wallace; Kirsch, 1877, *Mitt. Mus. Dresden* 1: 112.

Papilio albinus var. *sekarensis* Honrath, 1885, *Berl. ent. Z.* 29: 275.

Type locality: New Guinea (? Humboldt Bay).

Fore wing with pale band reduced to a series of subapical spots or absent; hind wing pale band very broad, narrowing towards tornus, present or absent in space 1b; tail present; hind wing underside with red spots often reduced, blue spots absent.

Male genitalia (Fig. 4) with apical plate of clasper broad and knob-like, not serrate.

Distribution: Two subspecies are recognised:—*P. a. albinus* lacks any pale fore wing markings and occurs in West Irian and north-west New Guinea; *P. a. lesches* Godman and Salvin has subapical fore wing pale spots present and occurs in southern Papua and adjacent areas of New Guinea.

Immature stages: Mature larva green with ventro-lateral longitudinal stripes and small tubercles on 9th abdominal segment; pupa smooth, green with broad ventro-lateral pinkish stripes (Straatman, pers. comm.). Larval food plants Rutaceae (D'Abbrera, 1978).

Papilio hypsicles Hewitson, stat. rev.

Papilio hypsicles Hewitson, 1868, *Exot. Butt.* 4: t. 9. f. 29.

Papilio canopus hypsicles Hewitson; Rothschild, 1895, *Novit. zool.* 2: 341.

Type locality: New Hebrides.

Fore wing with pale band present (rarely absent); hind wing pale band narrow, entire; tail present; hind wing underside with red spots present, often not in a complete series, and blue spots present, normally in a complete series.

Male genitalia (Fig. 5) with apical plate of clasper broad and distally serrate.

Distribution: Restricted to the New Hebrides.

Immature stages: Not described.

Comments: This species has nothing to do with *canopus*, with which it is generally associated, nor with *fuscus*. In male genitalic characters it is closest, surprisingly, to *woodfordi*, a relationship which makes sense in the light of distribution patterns of the two species. Although superficially similar to *canopus*, the wings are narrower, due to shorter discoidal veins, and the pale bands are further from the wing margin; this is especially noticeable in the

fore wing, where the pale band is almost vertical for most of its length in *hypisicles* and distinctly curved in *canopus*.

Papilio woodfordi Godman & Salvin

Papilio woodfordi Godman & Salvin, 1888, *Ann. Mag. nat. Hist.* (6)1: 100.

Type localities: Alu and Fauro Is. (Solomon Islands).

Fore wing pale band entire or reduced; hind wing pale band relatively broad, entire; tail reduced to a tooth; hind wing underside with red and blue spots generally present, red spots usually a complete series.

Male genitalia (Fig. 6) with apical plate of clasper broad and distally serrate.

Distribution: Restricted to the Solomon Islands. Five subspecies are currently recognised:—*woodfordi* (Bougainville and Shortland Is.); *choiseuli* Rothschild (Choiseul); *ariel* Grose-Smith (Santa Isabel); *laarchus* Godman and Salvin (New Georgia group) and *ptolychus* Godman and Salvin (Guadalcanal and Florida Is.). Racheli (1980) also records the species from Malaita.

Immature stages: Mature larva green, with very short tubercles on prothorax and 9th abdominal segment and some faint markings; pupa smooth, dark grey to black (Straatman, pers. comm.). Larval food plants Rutaceae.

Comments: Despite its distinctive appearance, the affinities of this species are clearly with *albinus* and *hypisicles*, particularly with regard to the male genitalia.

P. ponceleti Le Moul't, a possible hybrid between *woodfordi* and *fuscus*, was discussed by Racheli (1980).

Phylogeny and Biogeography

Members of the *fuscus* group show pattern characteristics typical of several groups of south-east Asian swallowtails, i.e. a basic black and yellow (or white) pattern which may or may not become modified by mimicry. The species contained within this overall grouping correspond to Munroe's (1961) Series 1 of his Subsection A, Section II, minus the *machaon*, *xuthus* and *demoleus* groups and subgroup (b) of his *demolion* group. The remaining species form a monophyletic section within the subgenus *Princeps* Hübner (Hancock, 1978, 1979).

The *fuscus* group itself is most closely related to the *aegeus/godeffroyi* assemblage, the mature larva of these three groups lacking both the metathoracic dark band and eye-spots as well as the "typical" smooth, green with brown bands pattern characteristic of the section. The *fuscus* group differs from the other two in having a smooth pupa and in possessing few tubercles in the mature larva. The *aegeus* and *godeffroyi* groups have a rough pupa and further development of tubercles in the mature larva. The additional tubercles in these two groups are undoubtedly secondary; they are perhaps

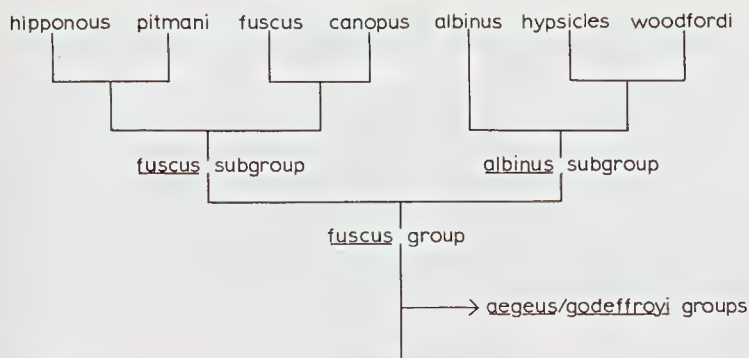


Fig. 7. Proposed phylogenetic relationships of the species of the *Papilio fuscus* group.

homologous to the abdominal pale spots of the *fuscus* group. The *aegeus* and *godeffroyi* groups are further united by the structure of the male genitalia, in that the clasper, whilst being similar to that of the *fuscus* group, has an additional, median, serrate lobe or prominent tooth. The *godeffroyi* group represents a Pacific offshoot of the Papuan *aegeus* group.

The *fuscus* group thus appears to have arisen as the sister-group to the *aegeus/godeffroyi* assemblage, the former most likely in Sundaland, the latter in New Guinea, following dispersal of an ancestral species from south-east Asia. In the Papilionidae, dispersal between south-east Asia and New Guinea appears to have been unidirectional, from west to east, no examples of Papuan-centred species or groups having extended westwards beyond the Moluccas, whereas several waves of dispersal appear to have brought western-centred groups into the Papuan region (Hancock, 1978).

A suggested initial scenario has the *fuscus* group differentiated in Sundaland and the *aegeus/godeffroyi* assemblage in the Papuan region. The sister-lineage of these three groups, comprising most of the remaining species in this section (the *demolition* group probably diverged earlier), and represented initially by the *helenus-nepheles* assemblage, differentiated in south-east Asia, outside Sundaland.

From Sundaland there was a further dispersal to New Guinea of many groups of Papilionidae, including the *fuscus* group, which became established there as the *albinus* subgroup, leaving the *fuscus* subgroup in Sundaland. From New Guinea (*albinus*) the group dispersed to the Solomons and New Hebrides, differentiating as *woodfordi* and *hypsicles* respectively. It appears likely that *hypsicles* reached the New Hebrides via the Solomons whereas other Pacific species [e.g. *godeffroyi* group, *Graphium gelon* (Boisduval), *P. montrouzieri* Boisduval] appear to have dispersed from south-east Papua to New Caledonia and beyond, avoiding the New Hebrides. A further example of

Solomons to New Hebrides dispersal is seen in *Graphium sarpedon* (Linnaeus), in recent times (Gross, 1975).

The Sundaland population, meanwhile, spread to Indo-China as *pitmani* and from there to the Philippines as *hipponous* (or *vice versa*), leaving *fuscus*, which subsequently reached the Lesser Sundas as *canopus*. The species of each subgroup are allopatric; only *fuscus*, a highly dispersive species that has extended throughout New Guinea to the Solomons and north-east Australia, occurs sympatrically with species of the *albinus* subgroup. From the Lesser Sundas, *canopus* reached north-western Australia.

The suggested phylogenetic relationships of the species are shown in Fig. 7.

Acknowledgements

This paper is a continuation of studies begun in the Department of Entomology, University of Queensland, and I thank Dr T. E. Woodward for his advice and guidance during the course of these initial studies. I thank Dr I. F. B. Common (A.N.I.C., Canberra), Mr E. C. Dahms and Dr G. B. Monteith (Queensland Museum) for the loan of specimens in their care, Dr S. A. Ae (Japan) for providing material of *P. hipponous*, Major A. Bedford Russell (U.K.) for supplying photographs and data of *P. pitmani* from Vietnam, Mr T. G. Howarth, formerly of British Museum (Natural History), for access to material in his care, and Mr R. Straatman (Australia) for information on life histories.

References

- Ae, S. A., 1977. Immature stage and genetics of *Papilio hipponous* (Lepidoptera: Papilionidae). *Trans. lepid. Soc. Japan* 28(4): 147-150.
- Ae, S. A., 1979. The phylogeny of some *Papilio* species based on interspecific hybridization data. *Syst. Ent.* 4: 1-16.
- Common, I. F. B. and Waterhouse, D. F., 1981. *Butterflies of Australia*. 2nd edition. Angus and Robertson, Sydney. 682 pp.
- D'Abrera, B., 1978. *Butterflies of the Australian region*. 2nd edition. Lansdowne, Melbourne. 415 pp.
- Dubois, E. and Salvaza, R. V. de, 1921. Contribution à la faune entomologique de l'Indochine française; familles Papilionidae, Pieridae et Danaidae. *Faune ent. Indo-Chine jr.* 3: 7-26.
- Gross, G. F., 1975. The land invertebrates of the New Hebrides and their relationships. *Phil. Trans. R. Soc. (B)* 272: 391-421.
- Hancock, D. L., 1978. *Phylogeny and biogeography of Papilionidae (Lepidoptera)*. Unpubl. M.Sc. thesis, Univ. of Queensland, Brisbane.
- Hancock, D. L., 1979. The systematic position of *Papilio anactus* Macleay (Lepidoptera: Papilionidae). *Aust. ent. Mag.* 6(3): 49-53.
- Munroe, E., 1961. The classification of the Papilionidae (Lepidoptera). *Can. Ent. Suppl.* 17: 1-51.
- Racheli, T., 1980. A list of the Papilionidae (Lepidoptera) of the Solomon Islands, with notes on their geographical distribution. *Aust. ent. Mag.* 7(4): 45-59.
- Straatman, R., 1963. A hybrid between *Papilio aegeus aegeus* and *Papilio fuscus capaneus*, with a note on larval food plants. *J. lepid. Soc.* 16: 161-174.